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Slow community responses but rapid species responses 14 years after alpine turf transplantation among snow cover zones, south–central New Zealand☆

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ABSTRACT

Alpine ecosystems are particularly vulnerable to the impact of global climate change. Depth and duration of seasonal snow cover are major drivers of variation in alpine plant community composition, so a reduction in snow cover as a result of climate change would expose plants that are currently protected by snow in winter and spring to greater extremes of temperature and increased risk of frost damage. We reciprocally transplanted 64 intact 60 cm × 60 cm × 10 cm (minimum depth) turves of alpine vegetation among four topographic zones on the Rock and Pillar Range, south-central South Island, New Zealand to investigate how shifts along a snow cover gradient affected plant growth, survival and community composition. The four zones: late-melting snowbed and early-melting snowbed in depressions, moderately exposed leeward upper slopes dominated by herbfield, and extremely exposed summit plateau dominated by cushionfield, differed in winter and spring snow cover. As expected, the highest species losses occurred in turves transplanted to very different zones e.g. late snowbed to summit plateau and vice versa. However many snowbed species still survived on the summit plateau seven years following transplantation. The degree to which turves had been colonised after seven years was significantly related to transplant zone rather than turf origin or original species richness; turves transplanted to the most species-rich zones were affected most by colonisation. Measurements of leaf production over three years in three focal *Celmisia* species (Asteraceae), characteristic of the herbfield on leeward slopes, and early and late snow-beds, showed that the late snowbed specialist suffered significantly reduced growth when transplanted to more exposed sites, but its survival was more affected by invertebrate herbivory rather than the direct effects of exposure. The cosmopolitan focal lichen species *Thamnolia vermicularis*, monitored over 14 years, rapidly colonised turves transplanted to cushionfield on the exposed summit plateau, where this and other lichens are abundant, but equally rapidly declined in turves transplanted to snowbeds. These findings add to a growing body of evidence that biotic interactions and species-specific traits will be critical drivers of alpine vegetation change under future climate scenarios.

1. Introduction

Alpine and polar ecosystems are likely to be particularly vulnerable to the impact of global climate change; global increases in air temperature and reduction in snow, ice and permafrost are strongly supported both by climate models and observation (IPCC 2014). However, our understanding of the impact of climate change on alpine areas around the world is less clear than our understanding of climate change in polar regions, due to the effects of temperature, precipitation, topography and geography on the behavior of snow (Gobiet et al., 2014; Musselman et al., 2017). Levels of snow cover in European and western North American mountain regions are significantly decreasing (Mote et al., 2005; Gobiet et al., 2014), and likewise, both maximum snow depth and total snow fall has declined in the Australian Alps (Fiddes et al., 2015). However, in the South American Andes, while the length of the core snow period has decreased generally, snow cover has significantly decreased only in northern portion of the range and instead increased in the southern Andes (Mernild et al., 2017).

Globally, increasing temperatures are likely to reduce the extent of alpine habitats, meaning that alpine species unable to migrate to suitable microclimatic niches, are likely to face competition from invading plant species from lower elevations (Halloy and Mark 2003; Hülber et al., 2011; Pauli et al., 2012; Alexander et al., 2016). Actual and experimental increases in temperature have been shown to correlate with changing plant species abundances and distributions (Walker et al., 2006; Cannone et al., 2007; Sebastià et al., 2008; Elmendorf et al., 2015). However, in topographically diverse alpine landscapes the availability of climatic microrefugia will likely provide a buffer against the impacts of warming temperatures (Scherrer and Körner 2010; Patsiou et al., 2014). In addition, a surprising number of alpine species show high levels of phenotypic plasticity (Frei et al., 2014; Sedlacek et al., 2015) and considerable resilience to environment stressors beyond their realised climatic niche (Bannister et al., 2005; Venn et al., 2013). These studies and others, together strongly connect with an emerging theme in the alpine climate change research field; that climate change impacts in alpine regions cannot be readily predicted from large scale climate models of communities. Rather, region-specific interactions between environmental factors, individual species traits, interactions between species, and indirect effects, are paramount in determining outcomes (Debouk et al., 2015; Farrer et al., 2015; Guittar et al., 2016; Alexander et al., 2016).

Variation in the depth and duration of seasonal snow cover is a major driver of alpine plant community composition, and modifications to that cover can produce changes in plant species distributions even over relatively short spaces of time (Carbognani et al., 2014; Mark et al., 2015). Warming temperatures in alpine regions are likely to alter patterns of seasonal snow cover, amount of precipitation falling as rain instead of snow and spring melt water (Lapp et al., 2005; Hendrikx et al., 2012; Gobiet et al., 2014; Klein et al., 2016; Musselman et al., 2017). Seasonal snow cover insulates and protects the underlying vegetation from sub-zero temperatures and damage from wind and frost (Bannister et al., 2005); long-lying snow cover not only acts as an insulator, but also significantly influences soil moisture levels due to the delayed release of melt-water (Sedlacek et al., 2015; Musselman et al., 2017). Furthermore, the timing of release from snow can also significantly delay phenological events such as leaf expansion and flowering (Björk and Molau 2007; Petraglia et al., 2014; Sedlacek et al., 2015), with consequential effects on the availability of resources for herbivores and pollinators (Björk and Molau 2007; Forrest and Thomson, 2011). These effects of snow cover lead to strong correlations between its presence and duration, and variation among alpine species in life-history, growth rate and functional traits (Callaghan et al., 2004; Jonas et al., 2008; Mark et al., 2016; Wheeler et al., 2016). In addition, persistent snowbeds, which are areas that, due to topography, accumulate deep winter snow, usually support a range of species not present elsewhere (Carbognani et al., 2012; Carbognani et al., 2012; Mark et al., 2016). While topographic variation is still likely to provide a mosaic of microclimates, snowbeds will be particularly threatened by spatial reduction and shifts in microclimate (Björk and Molau 2007; Matteodo et al., 2016).

The aim of this study was to investigate the long term impact of altered snow cover on alpine plant community composition on an isolated mountain range in south-central South Island, New Zealand, using reciprocal transplantation of intact plant communities along a natural gradient of snow cover. Transplantation is a powerful, but still relatively uncommon, method for directly testing the impact of altered environmental conditions and potentially novel biotic interactions on species and communities (Alexander et al., 2016; Nooten and Andrew 2017). Within a natural snow cover gradient we aimed to expose alpine species and communities to conditions representing likely and extreme levels of altered snow cover under future climate scenarios. Natural treeline in southern New Zealand is c.1200 m a.s.l. (above sea level) (Cieraad and McGlone 2014). Climate change models currently predict stable to increased precipitation in central and eastern areas of southern

New Zealand, but up to 22% reduction in peak snow accumulation below altitudes of 2000 m a.s.l. due to more precipitation falling as rain rather than snow (Mullan et al., 2008; Hendrikx et al., 2012). The New Zealand alpine flora shows a high level of regional and local endemism (c.93%), with highest species richness in the northern and southern regions of South Island. The alpine lichen flora is also very diverse, containing many bipolar species that are also found at high latitudes and altitudes in the Northern Hemisphere (Galloway and Aptroot 1995; Mark, 2012). Specialist alpine plant and lichen species are particularly associated with exposed habitats such as cushionfields and fellfields, characterised by mat-forming vegetation and rocky ground subject to freeze-thaw cycles respectively, as well as persistent snowbeds (McGlone and Heenan 2013). Our study aimed to quantify the resilience of such species and their constituent communities to altered snow regimes by additionally investigating the growth responses of focal species. We predicted that species that are restricted to particular zones along an exposure gradient would be most affected by changes in snow cover as a consequence of transplantation.

2. Methods

2.1. Study area

This study was carried out in the alpine zone on the Rock and Pillar Range (45° 25′ 32″ S, 170° 04′ 15″ E) South Island, New Zealand. The Rock and Pillar Range is one of a series of block faulted, chlorite schistose ranges in Central Otago, with a steeply sloping, heavily dissected, south-eastern scarp face and a summit plateau reaching 1450 m a.s.l. at its highest point. Subalpine shrub species and tall tussock (bunch) grasses occur in scattered patches up to c. 1280 m a.s.l., above which alpine herbfield and cushionfield dominate (Fig. 1A). The climate of the Rock and Pillar Range is somewhat maritime as it is 50 km from the Otago coast, but frosts can occur at any time of the year; Bannister et al. (2005) recorded a mean daily minimum air temperature of −0.33° C, an extreme daily minimum of −10.08° C in the same study area, and 42% of days with subzero air temperatures over a 16-month period (February 2003–June 2004). Annual precipitation exceeds 1000 mm, fog and low cloud are common and soil moisture levels remain close to field capacity throughout the growing season (Bliss and Mark 1974; Holdsworth and Mark 1990). Snow can fall at any time of the year, predominantly during southerly storms, and is extensively redistributed by the prevailing westerly winds, which average 7.9 ms^{-1} at 2 m above ground level, reducing to 2–3.5 ms^{-1} at ground level on the summit plateau, and 1.5–2.5 ms^{-1} at ground level on upper leeward slopes (Bliss and Mark 1974). Snow depth and duration vary consistently with topography; winter snow cover on the summit plateau varies between 0 and 0.5 m in depth due to extensive snow redistribution, whereas leeward upper slopes and snowbeds as little as 40 m below the summit plateau, accumulate snow throughout winter to depths of 0.5–4 m and up to 7 m, respectively (Talbot et al., 1992). Winter snow begins to accumulate from mid-May on leeward slopes and in snowbeds. The date that each zone is released from snow cover can vary by several days between successive years, but varies significantly more among zones, with snow in snowbeds persisting more than 50 days longer than on the summit plateau (Talbot et al., 1992). Snowmelt in all zones is usually completed by early– to mid–December.

Alpine vegetation patterns on the Rock and Pillar Range are strongly influenced by variation in snow depth and duration (Bliss and Mark 1974; Talbot et al., 1992). The exposed summit plateau is dominated by very low cushion-mat vegetation with a high abundance and diversity of lichens. The leeward slopes support a low diversity herbfield featuring large patches of *Celmisia viscosa* (Asteraceae), which has 5–8 cm long leaves coated in an epimanool-rich exudate that may provide protection from herbivores and desiccation (Sansom et al., 2013). In contrast, the vegetation of snowbeds is characterised by comparatively high species richness and diversity (Talbot et al., 1992; Table 1). Two

Fig 1. The study area, Rock and Pillar Range, South Island, New Zealand. (A): Catchment 1 showing the relative location of the four topographic zones; (B): late snowbed zone in catchment 2 with an excavated turf containing *Celmisia haastii* var. *tomentosa* ready for transport to its new location. Inset shows the location of the study area in relation to Dunedin, south–eastern South Island.

further *Celmisia* species are restricted to these snowbeds; the summer-green *C. prorepens* occurs in early-melting snowbeds, growing in loose mats with sticky leaves up to 5 cm long and the Rock and Pillar's endemic variety *tomentosa* of *C. haastii* is restricted to late-melting snowbeds, growing in small to large patches with leaves up to 4 cm long (Fig. 1B; hereafter referred to as *C. haastii*). These three *Celmisia* species served as focal species in this study.

2.2. Design of transplant experiment

In the 2002–03 growing season we selected two adjacent south-easterly facing catchments, i.e. exposed to at least some direct sunlight from sunrise to early afternoon, on the upper slopes of the range (catchment 1: 45° 25′ 02″ S, 170° 05′ 05″E, alt. range 1280–1365 m a.s.l; catchment 2: 45° 25′ 05″S, 170° 04′ 45″E, alt. range 1345 –

1380 m), and transplanted two 60 cm × 60 cm × 10 cm deep (min.) turves from each of four topographic zones, reciprocally into all four zones within each of the two catchments. All transplanted turves were surrounded by undisturbed vegetation and their surface was level with that of the surrounding undisturbed community. The four topographic zones consisted of the summit plateau above each catchment, which is dominated by lichen-rich cushionfield, the leeward upper slopes of each catchment, which is dominated by herbfield, early snowbed in shallow depressions/gullies within each catchment, and late snowbed in deep depressions/gullies within each catchment. Two control turves were also excavated and relocated within each topographic zone of each catchment. Vegetation for excavation from the herbfield on leeward slopes and also from snowbeds was selected to include their characteristic *Celmisia* species. The areas available for excavation were constrained by the need to avoid large rocks and obtain a turf of 10 cm

Table 1

Plant community characteristics of topographic zones differing in snow cover, in two catchments on the Rock and Pillar Range, South Island, New Zealand. Species richness is the mean (std. dev.) number of vascular and nonvascular plant species in 0.25 m² turves. Unique species are restricted to one zone within a catchment but may or may not be in the same zone in the other catchment. Snow lie is given in days between first persisting snow fall and time of last snow melt, although in some zones winter snow cover is not continuous. The value in brackets is the percent reduction in snow lie compared to the late snowbed zone within each catchment. NA: not available, as snow lie in 2004 was only measured in catchment 1 and equipment failure resulted in the loss of leeward slope data.

	Species richness	Unique species	2003 winter snow lie (days)	2004 winter snow lie (days)
Catchment 1				
Summit plateau	14.75 (3.632)	10	101 (48.5%)	100 (61.2%)
Leeward slope	5.875 (1.965)	3	144 (26.8%)	NA
Early Snowbed	10.63 (3.967)	6	180 (8.2%)	179 (30.6%)
Late Snowbed	13.00 (3.742)	12	196	258
Catchment 2				
Summit plateau	13.88 (2.204)	16	109 (39.4%)	NA
Leeward slope	8.000 (2.398)	4	163 (9.4%)	NA
Early Snowbed	9.375 (4.151)	5	159 (11.7%)	NA
Late Snowbed	14.63 (2.826)	19	180	NA

minimum depth, but were randomly selected within these constraints and randomly allocated to one of the four topographic zones. Turves were excavated by hand and transported in custom-made trays to minimise disturbance (Fig. 1B). Each turf was watered once, immediately after transplantation. No further watering was undertaken for the remainder of the experiment.

2.3. Climate measurements

To record soil temperature differences among topographic zones, Optic StowAway temperature loggers (Onset Computer Corp., Bourne, MA) were buried horizontally 10 cm below the ground surface adjacent to the uppermost turf in each zone of each catchment after all turves were transplanted, and set to record temperature hourly. Dataloggers were removed and downloaded after 14 months and mean, minimum and maximum monthly temperatures calculated.

2.4. Plant community surveys

The initial abundance of all vascular and non-vascular plant species and lichens was assessed by counting the number of 10 cm x 10 cm grid squares each species occupied in the central 9 squares of a permanently marked, 50 cm x 50 cm area (25 squares) on each turf at the time of transplanting. In January 2010, turves were resurveyed, counting the number of grid squares occupied out of 25 in order to quantify peripheral colonisation of the turf by new species. The impact of transplantation on plant community composition was elucidated using nonmetric multidimensional scaling (NMDS). The positions of turves along two ordination axes, based on species count data, were calculated using the Chi-square distance measure. Data from the original survey in the 2002–03 season were analysed to examine the distinctiveness of plant communities naturally occurring in the four topographic zones and between the two replicate catchment systems. Data from the January 2010 survey, seven years after transplantation, were analysed to investigate shifts in compositional similarity among transplanted and control turves. Data from the intervening years are not presented here. Multivariate analysis of variance was used to test if the resulting axis

scores differed significantly with either turf source (original zone) or location (zone the turf was transplanted into). Analysis of covariance was used to test if persistence of original species or number of new species colonising after seven years was affected by source or location of turves, independent of original species richness.

2.5. Leaf production in Celmisia species

Responses of the focal *Celmisia* species to altered snow cover were assessed by measuring leaf production in each of the three seasons following transplantation (2003–04, 2004–05 and 2005–06). In each *Celmisia*-containing turf transplanted between or within zones (i.e. only turves sourced from the herbfield on leeward slopes, and from late and early snowbeds: the focal *Celmisia* species did not occur in the summit plateau cushionfield), three to five *Celmisia* shoots were marked with coloured pegs. If shoots died, replacement shoots in the same turf were marked if available. Five non-transplanted control shoots were also marked in each of the three *Celmisia*-containing zones adjacent to the uppermost turf in that zone. The leafy shoots of *Celmisia* species grow determinately, with new leaves continually produced from the stem apex throughout the growing season: over-wintering buds are absent in these and most indigenous species (Dumbleton 1967). Inflorescences arise from the axils of the previous season's leaves. In late spring (November) of each year, new season's leaves were counted, the youngest fully expanded leaf present was marked by removing the apical 5 mm of the leaf tip, and developing leaves above the marked leaf were counted. Plants were revisited approximately monthly throughout each growing season until early autumn (March-April) to count further leaf production and re-mark leaves as necessary. The number of leaves produced per shoot was averaged for each turf in each season, and analysed using a General Linear Model treating catchment as a block effect and season, location and species as fixed effects. All 2-way interactions were included in the final model but the 3-way interaction between season, location and species was omitted as it did not contribute significantly to the model. The effect of transplantation was analysed using a Paired T-test, comparing mean leaves per shoot per season for non-transplanted control shoots with the grand mean of leaves per shoot per season of the two turves transplanted within the same zone.

Many shoots of the late snowbed specialist *Celmisia haastii* were observed to suffer from invertebrate herbivory and died during the course of measurement of leaf production. A Chi-squared test for independence was used to examine whether shoot death occurred non-randomly in this species in relation to zone. All data were inspected for normality and homoscedasticity prior to analysis. Analyses were performed in SPSS v. 24 (IBM) and Statistix v.9 (Analytical Software).

2.6. Abundance of Thamnolia vermicularis

To assess the impact of altered snow cover on non-vascular species, the focal lichen species, *Thamnolia vermicularis* was surveyed in detail. *T. vermicularis* is a cosmopolitan, fruticose lichen, with white tubular thalli occurring either in isolation or as interconnected clumps. *T. vermicularis* occurs in alpine areas worldwide as two different chemical variants which differ in UV fluorescence (UV +, UV −) (Sato 1968; Thomson 1984; Kärnefelt and Thell 1995; Galloway 2007), but which have been shown by DNA analysis to be the same species (Lord et al., 2013). Colonisation can occur via wind-blown thalli (Pérez 1991), however this species also produces asexual fungal spores (conidia) capable of long distance dispersal (Lord et al., 2013). *T. vermicularis* is naturally abundant in the exposed cushionfield on the summit plateau of the Rock and Pillar Range and c. 95% of strands here are the UV-variant. *Thamnolia* is also found in moderate abundance in the leeward upper slopes, but is absent from areas of moderate and deep snow accumulation. Its abundance was assessed by counting the total number of thalli > 1 cm in length on all turves in March 2004, February 2011, and February 2017, roughly one, eight and 14 years after
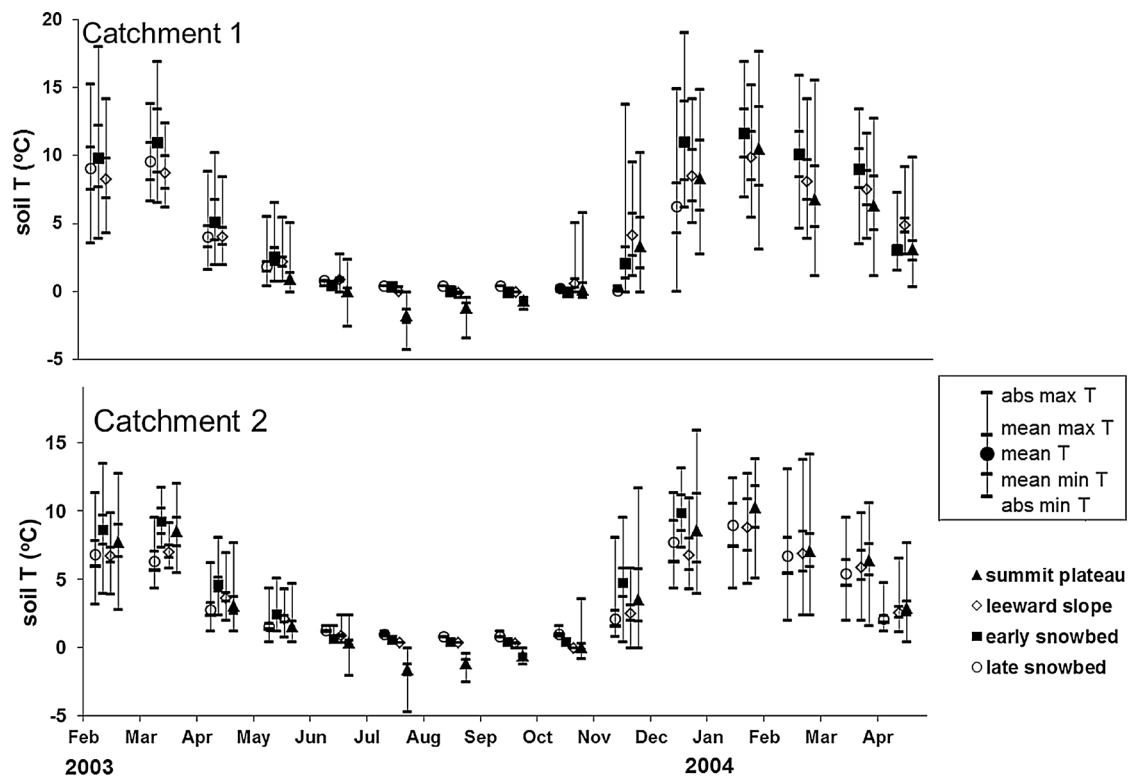
Fig. 2. Monthly soil temperatures in four topographic zones within two catchments on the Rock and Pillar Range, South Island, New Zealand, over the first 14 months of the transplant experiment. Data are missing for Feb–Apr 2003 on the summit plateau and Jan–Apr 2004 in the late snowbed zones of Catchment 1, and Jan-Apr 2004 in the early snowbed zone of Catchment 2 due to equipment failure.

transplantation. No attempt was made to separately count UV+ and UV- strands on turves. Changes in the abundance of *Thamnolia* thalli on turves one, eight and 14 years after transplantation was summed across the two replicate turves within each catchment, sharing the same source and transplant zone, and analysed separately for each catchment by Chi-squared tests of independence. Counts of thalli on turves transplanted into early and late snowbeds were summed to ensure expected values were greater than five.

3. Results

3.1. Climatic variation among topographic zones

Clear differences existed among topographic zones in the consistency of snow cover during winter and spring, and the likelihood of ground frosts. Over the first two winters of the experiment, the duration of snow cover on the summit plateau was reduced by 39–61%, and that of the leeward slopes was reduced by 9–27%, compared with the duration of snow cover in late snowbeds (Table 1). Mean monthly temperatures on the summit plateau were below zero throughout much of winter and early spring in both study catchments (Fig. 2), and the soil was exposed to freezing temperatures on almost 90% of winter days and more than 50% of spring days (Fig. 3). In contrast, soil temperatures on leeward slopes and in snowbeds barely dipped below zero over winter, and late snowbeds in particular were fully protected from ground level frosts throughout winter and spring (Fig. 3). Differences among topographic zones in mean monthly summer temperatures were small compared to the variation between mean minimum and mean maximum monthly temperatures within zones (Fig. 2).

3.2. Plant community responses

Plant community composition prior to transplantation showed very clear differences among topographic zones, with noticeably smaller

differences between the two study catchments (Fig. 4A). The most distinctive plant communities were those found on the summit plateau and in late snowbeds; the composition of vegetation in early snowbeds and on the leeward slopes was generally more similar. Seven years after transplantation, turves had become much less distinctive, but species composition was still significantly influenced by the original location of the turf (Wilks Lambda = 0.218, $F_{6,94} = 17.923$, $p < 0.0001$; Fig. 4B). The topographic zone into which the turf had been transplanted had significantly affected species composition after seven years (Wilks Lambda = 0.281, $F_{6,94} = 13.897$, $p < 0.0001$; Fig. 4C), but the effect of zone on species composition was not influenced by the original source of the turf (Wilks Lambda = 0.750, $F_{18,94} = 0.809$, $p > 0.05$).

The number of original species persisting in turves seven years after transplantation was not significantly related to either source or transplant zone (source: $F_{3,47} = 1.69$; transplant: $F_{3,47} = 0.28$; $p > 0.05$ for both; Fig. 5), but was significantly predicted by initial species richness (test for covariate $t = 6.820$, $p < 0.001$), and there was also a significant source × zone interaction ($F_{9,47} = 2.66$, $p < 0.05$, pooled catchments). Likewise the number of extinctions of original species in turves was not significantly related to either source or transplant zone (source: $F_{3,47} = 1.69$; transplant: $F_{3,47} = 0.28$; $p > 0.05$ for both; Fig. 5), but was significantly related to initial species richness (test for covariate $t = 4.55$, $p < 0.001$), and there was a similar source x location interaction ($F_{9,47} = 2.66$, $p < 0.05$, pooled catchments; F values identical as persisting + extinct species = initial species richness, the covariate). Both interactions were driven entirely by significant differences in original species persisting or going extinct on turves from the late snowbed zone transplanted to other zones (LSD pairwise comparisons, $p < 0.05$; Fig. 5). Colonisation showed no effect of source, location or initial species richness when all colonising species were combined (all F values < 2.5, covariate $t = -0.64$, all $p > 0.05$) because vascular and nonvascular species showed very different patterns of colonisation. Colonisation of transplanted turves by vascular plant species was significantly higher in vascular species–rich late
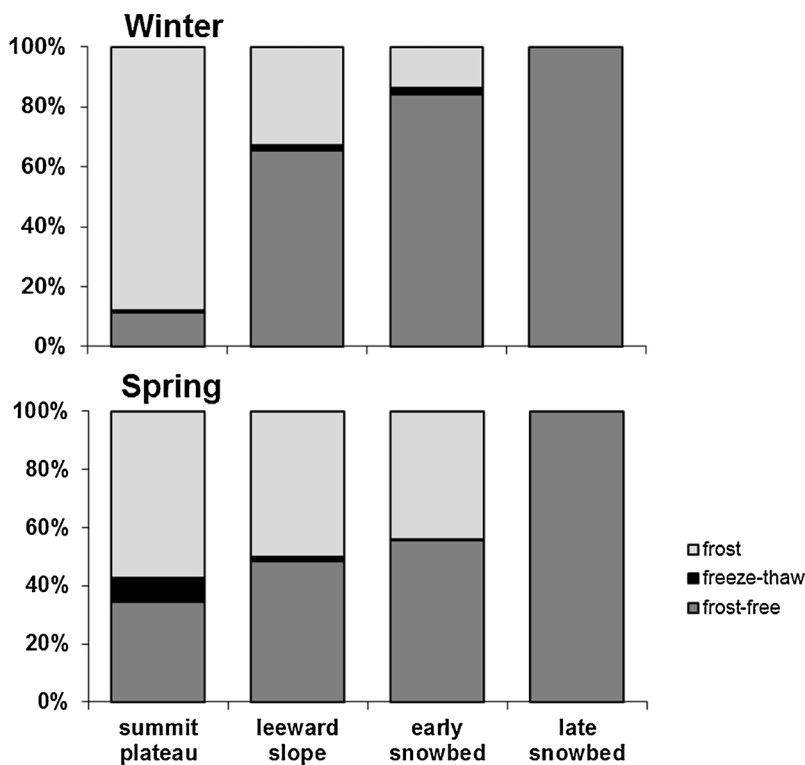
Fig. 3. Frequency of frosts, freeze-thaw days and snow-induced frost-free days in winter and spring, for four topographic zones differing in snow cover, Rock and Pillar Range, South Island, New Zealand. Values are averages for the two adjacent catchments.

snowbed (location $F_{3,47} = 4.03$, $p < 0.05$; Tukey's pairwise tests among locations $p < 0.05$), whereas colonisation by non-vascular species was significantly higher on turves in the lichen–rich summit plateau, following by turves on leeward slopes, and lowest in late snowbeds ($F_{3,47} = 13.19$, $p < 0.001$; Tukey's pairwise tests among locations, $p < 0.05$). Colonisation by either group of species was not affected by initial turf species richness (covariate $t = -0.25$, $p > 0.05$).

3.3. Responses of focal Celmisia species

A total of 303 shoots of the three focal *Celmisia* species were marked and monitored over the course of the three growing seasons; 69 of these survived one season or less, 105 survived two seasons and 129 were followed for the length of the study. Comparison of mean leaf production per shoot per season between transplanted turfs and non-transplanted control shoots indicated that transplantation did not affect leaf production ($T_{17} = 0.10$, $p > 0.05$). However, mean leaf production per shoot differed significantly among seasons, species and topographic zones, in addition to a significant species × zone interaction (Table 2). *A posteriori* tests found no significant difference in leaf production between the herbfield dominant *C. viscosa* and the early snowbed specialist *C. prorepens,* regardless of zone, but both produced significantly more leaves in every zone than *C. haastii*, the late snowbed specialist. Leaf production of the two snowbed species *C. prorepens* and *C. haastii* was, surprisingly, highest on the exposed summit plateau and most reduced in the herbfield on leeward slopes. No species performed best in its original environment.

Plant deaths in each growing season were significantly more frequent in *C. haastii* than in the other two *Celmisia* species for all zones combined (2003–04: $\chi^2 = 10.18$, df = 2, $p < 0.01$; 2004–05: $\chi^2 = 12.59$, df = 2, $p < 0.01$; 2005–06: $\chi^2 = 19.03$, df = 2, $p < 0.001$). In the first growing season after transplantation, the frequency of *C. haastii* deaths did not differ significantly among zones ($\chi^2 = 7.74$, df = 3, $p > 0.05$), however, in the following two growing seasons more *C. haastii* plants in the herbfield on leeward slopes died than expected and fewer died in the original late snowbed zone

(2004–2005 season: $\chi^2 = 22.36$, df = 3, $p < 0.001$; 2005–2006 season: $\chi^2 = 36.22$, df = 3, $p < 0.0001$). Many *C. haastii* deaths were associated with invertebrate damage to the leaves, which was identified in a parallel study by Long (2006) as most likely due to feeding by the large weevil *Irenimus posticalis* (Curculionidae), which is endemic to the Rock and Pillar Range and naturally found associated with *C. viscosa* on leeward slopes. Long (2006) conducted *in vitro* experiments on the relative palatability of the three focal *Celmisia* species studied here to *Irenimus posticalis* and found that *C. haastii* was most preferred. When *C. haastii* was transplanted to leeward slopes it was quickly targeted by *Irenimus posticalis* (Long, 2006).

3.4. Response of Thamnolia vermicularis

Colonisation by *Thamnolia vermicularis* of transplanted turves initially lacking this species was surprisingly rapid and significantly affected by location; when transplanted to the summit plateau, turves from other zones were colonised by up to 94 thalli after 14 months and up to 378 thalli after eight years (Fig. 6A,B). Fourteen years after transplantation to the summit plateau, the abundance of *Thamnolia* on snowbed turves was approaching that of control cushionfield turves, transplanted within the summit plateau (Fig. 6C). The abundance of *Thamnolia* also changed rapidly following turf transplantation to late snowbeds (Fig. 6), reducing by 35% in the 11 months from transplantation to early summer, and by a further 15% over the following three months of summer/autumn (mean number of thalli after 14 months = 257.9, std. dev. = 192), compared with control turves (mean = 518.7, std. dev. = 171). After eight years this lichen species had been virtually eliminated from turves in late snowbeds (mean = 1.750, std. dev. 2.872; Fig. 6B). However cushionfield turves from the summit plateau, that were transplanted to leeward slopes and early snowbeds, still supported *Thamnolia* after 14 years (Fig. 6C), although the abundance of thalli in the early snowbeds had reduced to 5.4% of that in control turves. Chi-squared tests of the effect of source and location on the sum of thalli on replicate turves were all highly significant (Catchment 1: 2004, $\chi^2 = 334.2$; 2011, $\chi^2 = 988.6$; 2017, $\chi^2 = 1431$; Catchment 2: 2004, $\chi^2 = 164.2$; 2011, $\chi^2 = 98.80$; 2017,
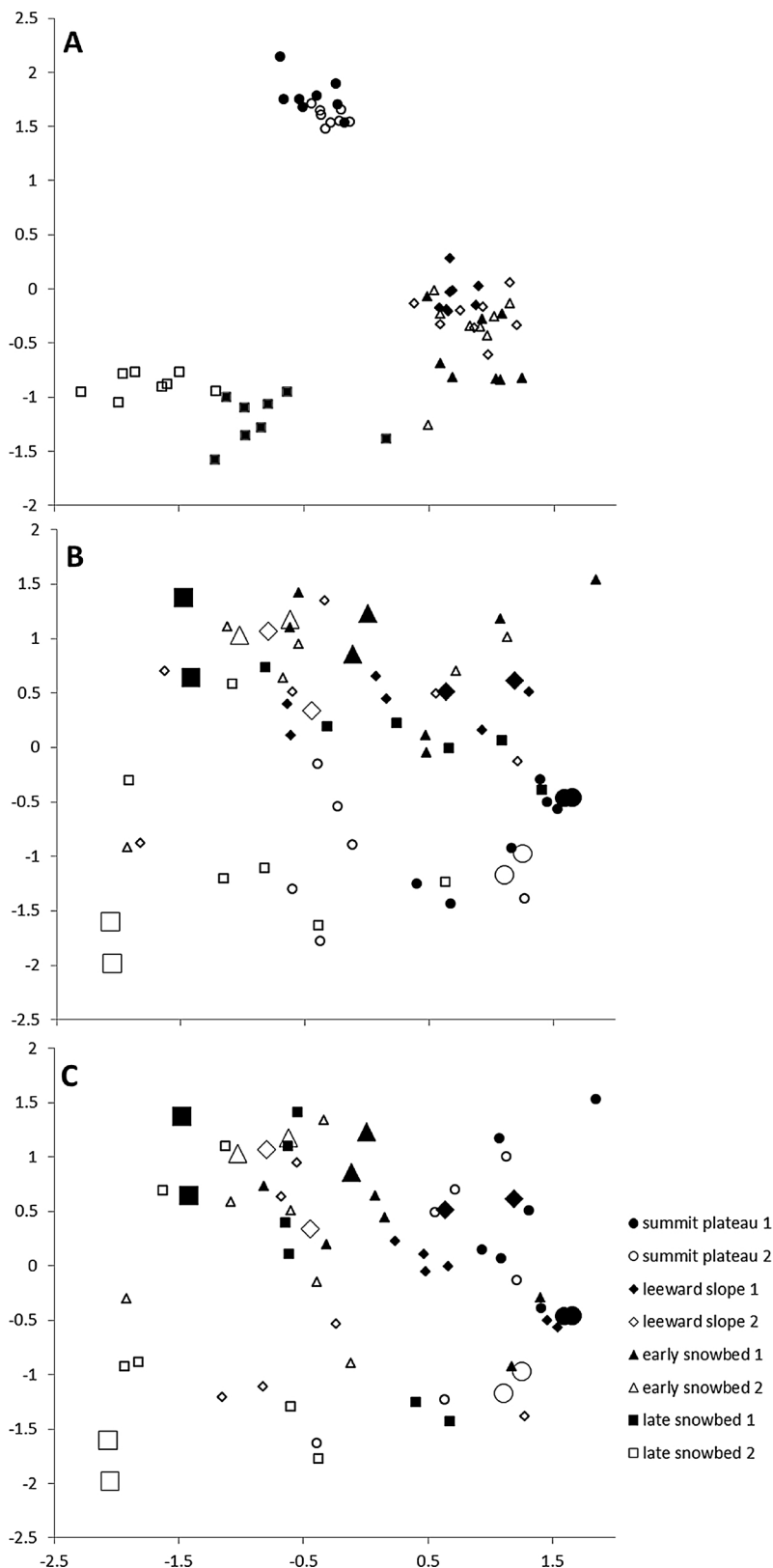
Fig. 4. Non-metric multidimensional scaling plots of variation in plant community composition in 16 turves from each of four topographic zones differing in snow cover, in each of two catchments on the Rock and Pillar Range, South Island, New Zealand. (A): Plant community composition in 2002, at the commencement of the transplant experiment, Stress = 0.2876 after 4 iterations, RSQ for matrix = 0.7977. (B) and (C): seven years after transplantation within and among four zones differing in snow cover. (B): symbols indicate topographic zone from which the turf originated; (C): symbols indicate topographic zone into which turf was transplanted. Larger symbols in B and C denote control turves transplanted within the topographic zone. Stress = 0.33234 after 4 iterations, RSQ for matrix = 0.70522.

- ● summit plateau 1
- ○ summit plateau 2
- ◆ leeward slope 1
- ◇ leeward slope 2
- ▲ early snowbed 1
- △ early snowbed 2
- ■ late snowbed 1
- □ late snowbed 2

$\chi^2 = 438.2$; $p < 0.01$, d.f. = 6 for all analyses).

4. Discussion and conclusions

Arctic and alpine plant communities throughout major parts of the world are undergoing significant transformation consistent with a changing climate (Grabherr et al., 1994; Gottfried et al., 2012; Elmendorf et al., 2015), but we still have a limited understanding of the direct and indirect processes driving these changes (Cooper, 2014; Farrar et al., 2015). Experimental warming, long term observation and space-for-time substitutions consistently highlight the critical role of species' climatic niches in determining responses to actual or inferred
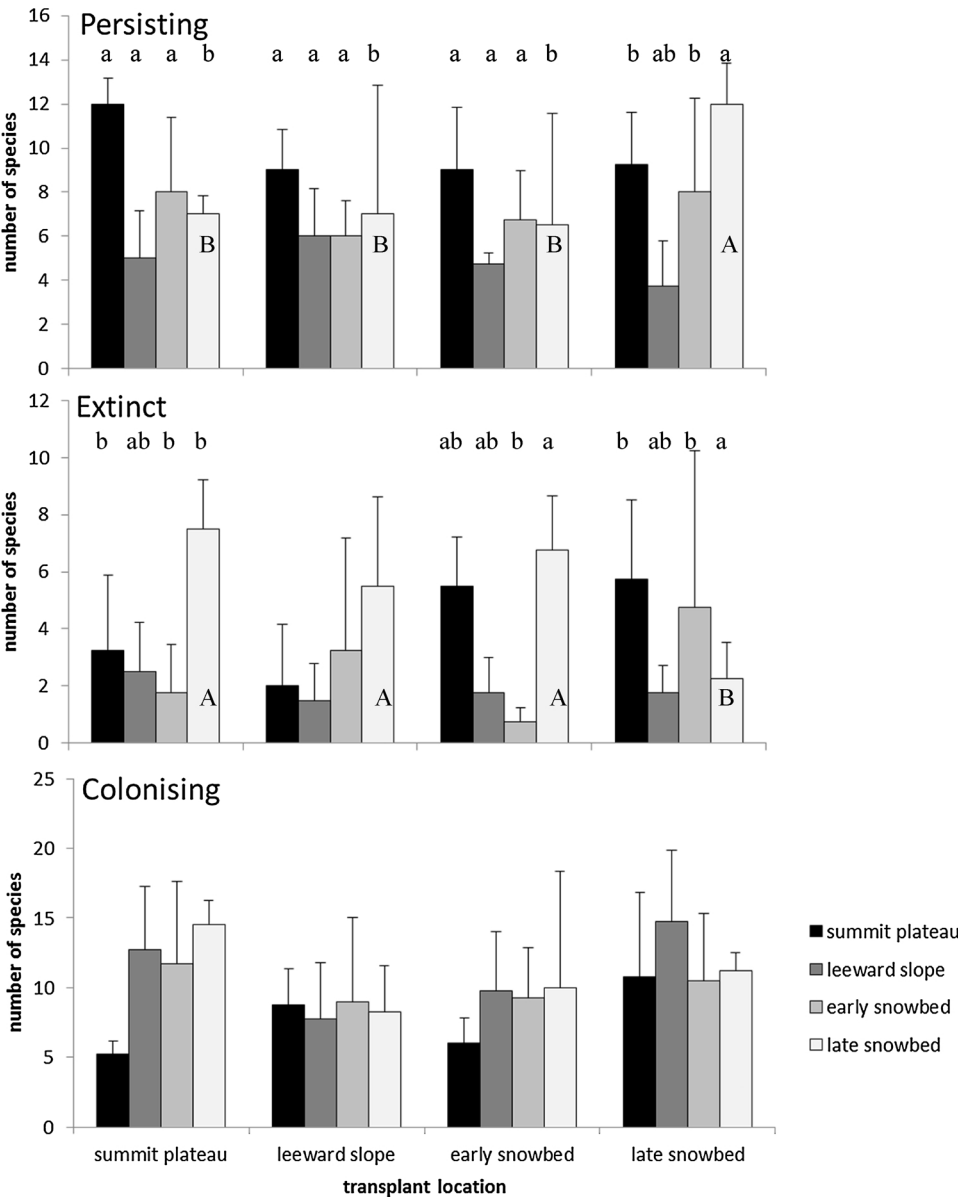
Fig. 5. The origin and fate of species recorded in turves seven years following transplantation among four topographic zones differing in snow cover on the Rock and Pillar Range, South Island, New Zealand. "Persisting" refers to species originally recorded on the turf at the time of transplantation. "Extinct" refers to original species that could no longer be found on the turves. All new species recorded since transplantation are in the "colonising" category. The legend indicates turf origin. Letters indicate significant differences (LSD, p < 0.05) following Analysis of Covariance, controlling for original species richness; lower–case indicate differences between turves within a topographic zone, upper–case indicate significant differences between zones for turves derived from the same topographic zone. Analysis of Covariance detected no differences in number of colonising species. Data are averages of four turves per source-location combination from two adjacent catchments. Error bars represent one standard deviation.

Table 2

General Linear Model analysis of mean leaf production per turf over three growing seasons in three focal *Celmisia* species transplanted into four topographic zones differing in snow cover on the Rock and Pillar Range, South Island, New Zealand. The two replicate catchments were treated as a block effect.

Model term	Mean Square	F, d.f.	p
Intercept	11195.83	$F_{1,119} = 1891.1$	< 0.001
Catchment	47.598	$F_{1,119} = 8.040$	< 0.01
Season	62.211	$F_{2,119} = 5.254$	< 0.01
Zone	185.63	$F_{3,119} = 10.452$	< 0.001
Species	1037.7	$F_{2,119} = 87.639$	< 0.001
Season × zone	56.716	$F_{6,119} = 1.597$	> 0.05
Species × zone	262.29	$F_{6,119} = 7.384$	< 0.001
Season × species	24.223	$F_{4,119} = 1.023$	> 0.05
Error	704.52		

climate change (Elmendorf et al., 2015). However, novel biotic interactions such as competition and herbivory are also emerging as important factors affecting the ability of species to survive *in situ* or migrate with changing climatic patterns (Olofsson et al., 2009; Hülber et al., 2011; Kaarlejärvi and Olofsson 2014; Alexander et al., 2016). Transplant experiments provide a means by which the effects of these

interactions can be assessed under natural conditions, yet such experiments are still rare. Our study is one of the few documenting the long–term fates of alpine species and communities following transplantation to different topographic zones along a snow cover gradient, and while we only studied change in two adjacent catchments, our inclusion of four topographic zones in each, in a reciprocal transplant design, allowed for relatively fine scale analyses of species and community responses.

To a certain degree in our study, environment accounted for the observed changes; the snowbed specialist *Celmisia haasti* showed the least growth and snowbed turves demonstrated the greatest number of species extinctions when transplanted to more exposed zones. While the snowbed communities studied here were richer in species and experienced warmer temperatures than in many northern hemisphere snowbeds (e.g. Hülber et al., 2011; Carbognani et al., 2014), our study confirmed that these communities can be strongly affected by reduced snow cover (Kipkeev et al., 2015; Matteodo et al., 2016), making them particularly vulnerable to climate change (Björk and Molau 2006). The difference in snow cover between our most protected late snowbed zone and most exposed summit plateau zone, at the time our experiment was established, was around two times the current predicted reduction in
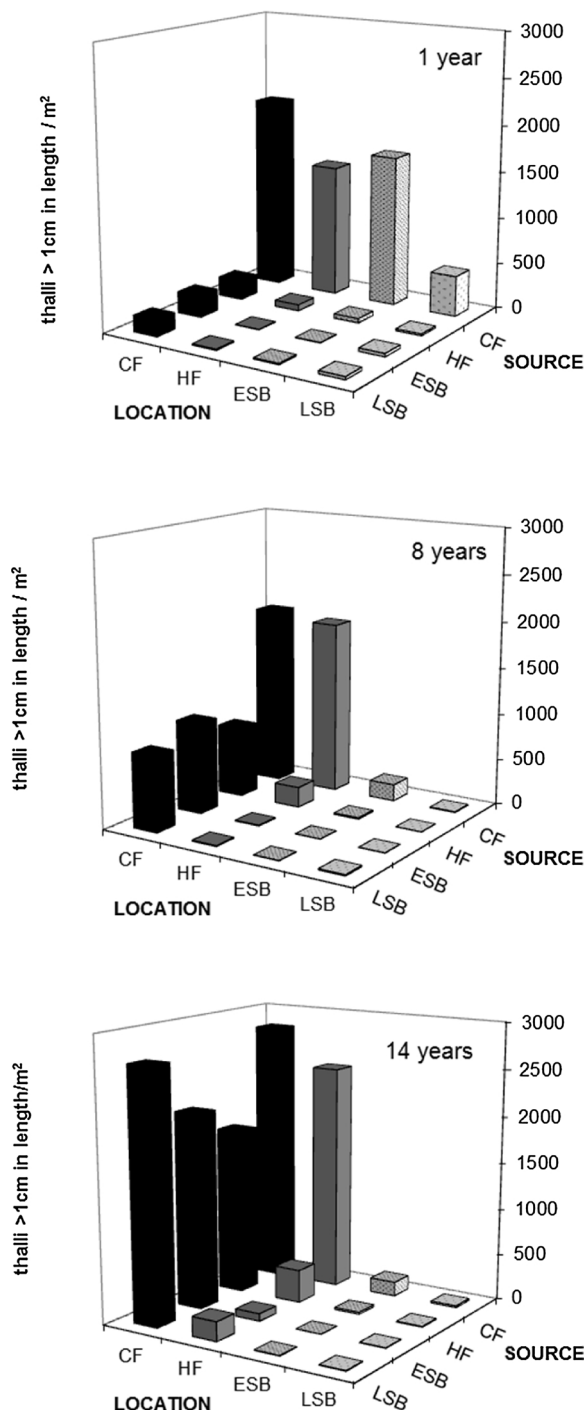
Fig. 6. Changes in the abundance of *Thamnolia vermicularis* thalli > 1 cm in length on turves transplanted within and among topographic zones differing in snow cover on the Rock and Pillar Range, South Island, New Zealand, one, eight, and 14 years after transplantation. Each bar is the sum of four replicate 0.25 m² turves. CF: summit plateau cushionfield, HF: leeward slope herbfield, ESB: early snowbed, LSB: late snowbed. Turves with the same source and location are controls that were relocated within the same vegetation type and topographic zone.

snow cover of 22% for alpine southern New Zealand under climate change projections (Mullan et al., 2008; Hendrikx et al., 2012), so represents an extreme scenario. However, differences between the early and late snowbed and leeward slope zones represent realistic levels of future snow cover reduction. Given the current climate change predictions, it is highly unlikely that snowbeds in our study area will completely disappear, but they are likely to contract and fragment,

exposing marginal areas. It is reassuring then, that a number of snowbed species were persisting in more exposed zones even after seven years, suggesting that these plant communities may have some inherent resilience to altered snow cover. A growing number of studies, both in New Zealand and elsewhere, have found that alpine and arctic species can demonstrate broad tolerances beyond their apparent microclimatic niche, and respond individualistically to changes in temperature (Bannister et al., 2005; Hülber et al., 2011; Pieper et al., 2011; Venn et al., 2013; Frei et al., 2014; Sedlacek et al., 2015), therefore future plant community distributions are unlikely to be accurately modelled using species' current climate niches. It is highly likely, though, that further changes in species composition will be detected as we continue to follow the fate of our transplanted turves, as it is clear from this and other studies, that altered climatic conditions trigger both rapid responses and long term changes that are species- and process-specific (Pieper et al., 2011; Farrer et al., 2015; Cannone et al., 2007). Even 25 years following transplantation, the composition of alpine plant communities can still be adjusting to a novel environment, although the rate of change may decrease (Kipkeev et al., 2015).

A distinct advantage of transplant experiments, over *in situ* environmental manipulations such as soil warming, is that the transplanted species are exposed to potentially novel species, not just novel climatic factors (Alexander et al., 2016; Nooten and Andrew 2017). In our study system, biotic interactions are likely to be at least as important as abiotic factors in determining the survival of species under altered snow regimes. While increased exposure to freezing temperatures may have affected the survival of some snowbed species transplanted to the exposed summit plateau, Bannister et al. (2005) showed that *C. haastii* at least was capable of surviving even the harshest frosts recorded in that environment. For this plant species, exposure to increased herbivory seemed to be a critical factor in its decline following transplantation. Species-specific herbivory has been shown to counteract the effects of climate-related species range expansions through the preferential browsing of taller or faster growing species (e.g. Olofsson et al., 2009; Kaarlejärvi and Olofsson, 2014). However, in our study herbivory by an endemic weevil appears to have exacerbated the effects of altered environmental conditions. Quite likely this weevil is normally unable to access *C. haastii* due to phenological mismatch driven by differences in snow cover duration; thus a reduction in the extent of snow at critical times of the year could have serious implications for the survival of this, and other palatable species, in snowbed margins. Interactions with insects have been a critical force shaping the plant world (Schoonhoven et al., 2005) and exposure to new insect herbivores is likely to be an important component of plant survival under future climate conditions (Nooten and Andrew 2017). We strongly recommend that experimental controls restricting invertebrate, as well as vertebrate, herbivores are included in future transplant experiments in alpine areas, and also suggest that measures of invertebrate herbivore damage are explicitly included in monitoring methodologies such as GLORIA, which currently only recommends that grazing impacts by mammals be noted (Pauli et al., 2015).

The inclusion in our study of both vascular and non-vascular focal species allowed us to identify opposing effects of altered snow cover on species. *Thamnolia vermicularis* rapidly colonised turves transplanted to the lichen-rich, exposed summit plateau and equally rapidly declined when subject to increased depth and duration of snow cover in the snowbeds, generally matching other studies of lichen responses to increased snow cover (Bidussi et al., 2016). While a scenario of increasing snow cover is unlikely at our study site, it does highlight the potential value of this species as a global indicator of both increasing and decreasing snow cover. Lichens are the dominant photoautotrophs in high alpine and polar regions, often surpassing vascular plants in both species richness and abundance, and contributing key ecosystem services such as soil stabilisation and nitrogen capture (Ahti 1977; Kappen 2000; Cornelissen et al., 2001). Unlike many vascular plants, they are often small, discrete and easily translocatable, so are highly suitable as

indicators of climate change both *in situ* (Sancho et al., 2007) and in transplantation experiments (Bidussi et al., 2016). However, the use of cold-climate lichens as indicators of climate change is often hindered by their slow growth rates, for example McCarthy (2003) recorded growth rates of 0.26–0.41 mm/year for the cosmopolitan crustose lichen, *Rhizocarpon geographicum*. Foliose and fruticose lichens generally have higher growth rates than crustose lichens (Sancho et al., 2007); in keeping with this, we have recorded length increases of up to 5 mm in *Thamnolia vermicularis* thallus branches within a single growing season (Knight and Lord unpub. data). As *Thamnolia vermicularis* is globally widespread and distinctive, we strongly encourage alpine ecologists and environmental managers to include it in monitoring programmes, as a rapid and sensitive bioindicator that can be easily compared among alpine and arctic areas worldwide.

Long term transplant studies can provide detailed information not only concerning species' climatic tolerances and the impact of altered environmental conditions on growth and survival, but also provide insights into the types and significance of potential novel interactions that may emerge as species' ranges shift. These types of studies therefore offer ecologists and modelers critical information beyond that which can be provided by *in situ* climate manipulation experiments (e.g. Walker et al., 2006) and more rapidly than can be obtained from long–term monitoring (e.g. Gottfried et al., 2012). The impacts of climate change on alpine, or in fact any, species or communities, cannot readily be predicted from large-scale climate models when effects like novel competitive interactions and local species-specific herbivory are as important to species survival and compositional change as are environmental tolerances. We strongly encourage alpine ecologists to use transplantation, combined with herbivore and competitor exclusion treatments, to test the relative importance of climatic vs biotic interactions to species distributions. We also suggest that the identification of key functional traits and ecological strategies might be the best approach to explain and predict alpine species' responses to the complex web of interacting factors inherent in future climate scenarios (e.g. Mark et al., 2015; Debouk et al., 2015; Guittar et al., 2016), much as plant strategy schemes are now making sense of ecological variation among plant species and communities worldwide (Díaz et al., 2016).

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